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Cephalopods from the Stomachs of Sperm Whales taken off California

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Cephalopods from the Stomachs of Sperm Whales taken off California

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ABSTRACT

Cephalopod remains (beaks, bodies, and parts of bodies) were collected from the stomachs of 157 sperm whales (*Physeter macrocephalus*) taken off central California (lat. 37°–39°N). At least 24 species representing 14 families were identified. Frequencies of occurrence of the six most numerous taxa were *Moroteuthis robusta* 72.0%, *Gonatopsis borealis* 66.2%, *Histioteuthis dofleini* 36.9%, *Galiteuthis* spp. (including *G. phyllura* and *G. pacifica*) 36.3%, *Octopoteuthis deletron* 35.0%, and *Vampyroteuthis infernalis* 27.4%. One find of two *Mesonychoteuthis hamiltoni* beaks strongly suggests transequatorial migration by one large male sperm whale.

Introduction

Sperm whales (*Physeter macrocephalus*) feed mainly on medium to large cephalopods, which they apparently capture at depths ranging from several hundred meters to perhaps as great as 3000 meters (Rice 1989). The stomachs of sperm whales thus provide samples of a portion of the cephalopod fauna that can seldom be sampled by other methods. During the course of research on the life history and ecology of the great whales in the eastern North Pacific, Rice and Wolman (1970) examined 637 sperm whales taken in commercial shore-based whaling operations off central California (lat. 37°–39°N) during 1959–70. Rice (1963a,b) described the whaling operations and area off central California and illustrated the bathymetry of the ocean floor.

Initial examination of the cephalopod specimens collected from the stomachs of sperm whales began in the early 1960s. Rice (1963b) listed *Moroteuthis robusta*, *Gonatopsis borealis*, *Onychoteuthis* sp., *Octopus* sp., and unidentifiable squids. Rice and Wolman (1970) added an additional seven genera to the published record. Fiscus and Rice (1974) published a note on the finding of *Architeuthis* sp. in sperm whale stomachs. Fiscus completed the initial examination of the material in 1972, and a list of cephalopod taxa was prepared but not published.

During this period, selected material was sent to other cephalopod specialists for identification or confirmation of identification. These specialists are acknowledged in the individual species accounts. Fiscus took samples of squid beaks to the workshop on identification of cephalopod beaks held 1–12 June 1981 at the laboratory of the Marine Biological Association of the United Kingdom at Plymouth, England (Clarke 1986a). As a result of this workshop and discussions with the participants, most of the remaining unidentified beaks were identified. The entire collection was reexamined by Fiscus between 1983 and 1988; the results of this examination are presented in Table 1 and in the following species accounts.

In this report, we present our data on taxonomy and distribution of the taxa of cephalopods found in sperm whale stomachs. An analysis of the sperm whale's prey—which includes fishes and crustaceans as well as cephalopods—in relation to feeding ecology, sex, age, and social behavior of the whales, will be included in a forthcoming report by Rice and Wolman on the biology of the sperm whale in the eastern North Pacific.

Materials and Methods

Sperm whales were landed at the whaling stations of the Del Monte Fishing Company and the Golden Gate Fishing Company at Point San Pablo, Richmond, California. Whales were taken during all months except January, but the majority were taken May to November. Contents of the stomachs of 483 sperm whales were examined at least cursorily; however, because of the rapidity of the flensing operations and the need to gather other biological data, we were able to collect samples of cephalopod beaks from only 157 stomachs. All stomachs contained at least a few cephalopod beaks. The number of beaks collected from each stomach ranged from 1 to 57, and the total number of beaks was 2060 (not including beaks from whole specimens, crowns, and buccal masses). All of the remains collected represent a minimum of 1700 individual cephalopods.

These samples of whale stomach contents were fixed in 10% formalin or 70% ethanol or isopropanol, and brought back to the Marine Mammal Biological Laboratory (now the National Marine Mammal Laboratory, NMML) in Seattle. Fiscus began the examination of cephalopod material in the early 1960s. The samples were mostly represented by beaks, but fortunately some relatively intact specimens or crowns (heads with arms and tentacles) were included in the samples. After the whole bodies and heads were identified, the beaks were removed and compared with other beaks in the samples. Papers by Akimushkin (1965), Berry (1912), Clarke (1966), Pearcy (1965), Phillips (1933, 1961), and Verrill (1882) were most useful during initial stages of the study. Papers by Okutani and McGowan (1969) and Young (1972) were important sources of information on species of cephalopods present in the California Current system. Anderson (1978) and Talmadge (1967) listed species of cephalopods from Monterey Bay and northern California. Jefferts (1983, 1988) provided important new information on cephalopod distribution in the northeastern Pacific Ocean.

Cephalopod beaks were identified by comparison with vouchered beaks in the NMML collection and through the use of beak descriptions and illustrations (Clarke 1986a, Iverson and Pinkas 1971, Wolff 1984). Lower beaks are most useful in determining species of cephalopods; however, some upper beaks are characteristic of certain species or genera, and were used when possible.

Species Accounts

Classification and sequence of families and genera of cephalopods follows Clarke and Trueman (1988), who updated the list by Voss (1977). We identified 24 species representing 14 families of squids and octopods from the 157 stomach samples examined. For each, we have calculated frequency of occurrence and number of individuals (Table 1).

The following abbreviations are used throughout: **GL** = gladius length; **LRL** = lower rostral length; **ML** = dorsal mantle length; **NMML** = National Marine Mammal Laboratory.

Loliginidae

***Loligo opalescens* Berry, 1911** The occurrence of a single upper beak in the stomach of a sperm whale almost certainly represents a secondary occurrence, i.e., it was initially consumed by a larger cephalopod or fish which was in turn eaten by the whale. *Loligo opalescens* is a neritic species that occurs off central California throughout the year (Fields 1965). It is a schooling species, and we have found that it usually constitutes the bulk of the contents when it occurs in marine mammal stomachs. Hixon (1983) provided a detailed life history of this species, which moves to shallow inshore waters to spawn. In the commercial catch in Monterey Bay, California, the average ML of mature males was 150 mm and of mature females 140 mm. Large mature specimens in the NMML collection are in the size range 180–206 ML. This species is of major importance as prey to several species of shallow diving marine mammals found off central California, such as the northern fur seal (*Callorhinus ursinus*), Pacific white-sided dolphin (*Lagenorhynchus obliquidens*), and Dall's porpoise (*Phocoenoides dalli*) (Stroud et al. 1981, Kajimura 1984, Clarke 1986b); however, *L. opalescens* is not usually found at the depths at which sperm whales feed.

Enoploteuthidae

***Abraliopsis felis* McGowan and Okutani 1968** The presence of a single upper beak of this species in the stomach of a sperm whale must certainly represent a secondary occurrence. *Abraliopsis felis* is a schooling species, and we have noted that it is usually a major component of the contents when it occurs in marine mammal stomachs. This species is found in the waters of the California Current system, where it is mesopelagic to epipelagic (Jefferts 1983). Mature specimens may measure 60 mm ML. The species forms a regular part of the diet of the shallow diving marine mammals (Kajimura 1984, Stroud et al. 1981).

Table 1

Frequency of occurrence and number of individuals of cephalopods in the stomachs of sperm whales collected off central California.

Species	Frequency of occurrence				Number of individuals[1]			
	Family[2]		Species		Family		Species	
	N	%	*N*	%	*N*	%	*N*	%
Teuthida								
Loliginidae	1	0.6			1	0.07		
Loligo opalescens[3]			1	0.6			1	0.07
Enoploteuthidae	1	0.6			1	0.07		
Abraliopsis felis[3]			1	0.6			1	0.07
Octopoteuthidae	56	35.7			125	9.33		
Octopoteuthis deletron			55	35.0			124	9.25
Taningia danae			1	0.6			1	0.07
Onychoteuthidae	119	75.8			334	24.93		
Onychoteuthis borealijaponica			15	9.6			22	1.64
Moroteuthis robusta			113	72.0			312	23.28
Gonatidae	108	68.8			421	31.42		
Gonatus spp.			5	3.2			5	0.37
Gonatus pyros			3	1.9			5	0.37
Gonatus berryi			16	10.2			28	2.09
Gonatus sp. (cf. *G. fabricii*)			19	12.1			25	1.87
Gonatopsis borealis			104	66.2			352	26.27
Unidentifiable gonatids			4	2.5			6	0.45
Architeuthidae	11	7.0			11	0.82		
Architeuthis japonica			11	7.0			11	0.82
Histioteuthidae	73	46.5			207	15.45		
Histioteuthis spp.			13	8.3			34	2.54
Histioteuthis dofleini			58	36.9			164	12.24
Histioteuthis heteropsis			6	3.8			9	0.67
Ommastrephidae	5	3.2			7	0.52		
Dosidicus gigas			4	2.5			4	0.30
Unidentifiable ommastrephids			1	0.6			3	0.22
Chiroteuthidae	5	3.2			6	0.45		
Chiroteuthis calyx			5	3.2			6	0.45
Mastigoteuthidae	3	1.9			3	0.22		
Mastigoteuthis spp.			3	1.9			3	0.22
Cranchiidae	68	43.3			133	9.93		
Taonius pavo			2	1.0			2	0.15
Megalocranchia spp.			8	5.1			9	0.67
Galiteuthis spp.			39	24.8			72	5.37
Galiteuthis phyllura			12	7.6			18	1.34
Galiteuthis pacifica			11	7.0			15	1.12
Mesonychoteuthis hamiltoni			1	0.6			2	0.15
Unidentifiable cranchiids			9	5.7			15	1.12
Vampyromorpha								
Vampyroteuthidae	43	27.4			62	4.63		
Vampyroteuthis infernalis			43	27.4			62	4.63
Octopoda								
Octopodidae	11	7.0			26	1.94		
Octopus dofleini			11	7.0			26	1.94
Alloposidae	2	1.3			3	0.22		
Alloposus mollis			2	1.3			3	0.22
Total identified individuals[4]							1340	
Unidentifiable								
Histioteuthidae or Cranchiidae			67	42.7			318	
Megalocranchia or *Taningia*			4	2.5			7	
Cephalopoda			19	12.1			35	
Total unidentified individuals							360	
Total individuals							1700	
Total stomachs			157					

[1]Minimum number necessary to account for the remains from each stomach; for example, 3 upper beaks and 2 lower beaks are counted as 3 individuals.
[2]Family totals may be less than sum of species totals because some stomachs contained more than one species
[3]Probably secondary food item from stomach of sperm whale's prey species.
[4]Identified at least to family.

Octopoteuthidae

***Octopoteuthis deletron* Young, 1972** This species is represented mostly by beaks of 1–5 specimens per stomach; however, beaks from 12 specimens were found in one stomach. No flesh remains were found. LRL of 13 beaks measured 6.0–9.5 mm ($\bar{x}$ 7.1 mm). The species is mesopelagic to epipelagic in habit (Jefferts 1983, Roper and Young 1975) and is endemic to the California Current system. Clarke (1986a) stated that *Octopoteuthis* spp. are important in the diet of sperm whales in all but the coldest waters of the world.

***Taningia danae* Joubin, 1931** We found one lower beak with an LRL of 12.0 mm. No wing darkening was apparent even at this size. To our knowledge, no whole specimens of *T. danae* have been collected from the California Current system. The only published record for California is that of Condit and Le Boeuf (1984) who reported this species from the stomach of one elephant seal (*Mirounga angustirostris*); although not stated in their paper, M.R. Clarke (Mar. Biol. Stn. U.K., Plymouth, England) identified their specimen. Roper and Young (1975) stated that little is known of the depth range of this species; however, they cited one record from the stomach of a bottom-dwelling shark taken on hook-and-line at 1246 m. Clarke (1986a) indicated that this species is important in the diet of sperm whales in the Atlantic from lat. 40°S to 53°N and in the Pacific from lat. 40°S to 37°N. This species has been taken from the stomachs of sperm whales captured off the coast of Honshu, Japan (Okutani et al. 1976, Okutani and Satake 1978). Okutani (1974) listed 16 specimens taken in micronekton tows during the EASTROPAC expeditions from the eastern tropical Pacific.

Onychoteuthidae

***Onychoteuthis borealijaponica* Okada, 1927** This species is represented by beaks from 1–3 squids per whale stomach. No fleshy parts were present in the samples, but gladii were identified with GL in the size range 303–320 mm. LRLs of three beaks measured 3.0, 5.5, and 6.0 mm. The species is abundant in slope waters off central California, as indicated by its frequent occurrence in marine mammal stomachs (Kajimura 1984, Stroud et al. 1981), and ranges across the North Pacific from Baja California north and west to Japanese waters. It is mesopelagic to epipelagic, and at least part of the population migrates to the surface at night (Jefferts 1983). It forms an important part of the diet of the shallow diving marine mammals (Stroud et al. 1981, Kajimura 1984), and also is taken by the deep diving elephant seal (Condit and Le Boeuf 1984, Antonelis et al. 1987). Mead et al. (1982) found this species in four of five stomachs of archbeak whales (*Mesoplodon carlhubbsi*) that stranded on the southern California coast.

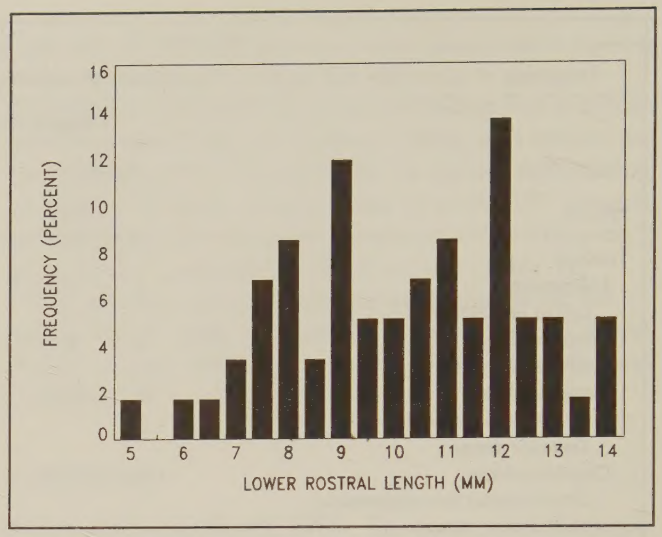

Figure 1
Lower rostral length-frequencies of 59 *Moroteuthis robusta* beaks from the stomachs of sperm whales taken off California.

***Moroteuthis robusta* (Verrill, 1876)** This large squid occurred more frequently (72%) than any other species in our survey. Most samples contained beaks of 1–7 squids; however, one sample contained beaks from 12 and another from 26 individuals. The characteristic cartilaginous end-cones of the gladii of this species are a conspicuous component of the stomach contents of most California sperm whales. Two whole squids were collected from sperm whale stomachs, one measuring 363 mm ML and the other ~1000 mm ML. Rice has examined (but could not preserve) many whole specimens measuring up to 1300 mm ML. Several crowns (head with arms and buccal mass) are also represented in the collection, as well as fragments of gladii and cartilaginous end-cones of gladii. LRLs of 59 beaks were in the size range 5–14 mm ($\bar{x}$ 10.1 mm) (Fig. 1). The same LRL range was found by Clarke and MacLeod (1980) in beaks they examined from the stomachs of sperm whales taken off western Canada. Roper and Young (1975), commenting on the depth occurrence of this species, stated that the upper limit of its distribution appears to be ~100 m. Most are taken in commercial bottom trawls at depths much deeper than this. Hochberg (1974), in summarizing capture records, stated that *Moroteuthis* lives near the bottom at depths of 200–600 m; he published records of six specimens taken by bottom trawl in the Santa Barbara channel at depths of 200–300 m. Jefferts (1983) reports a maximum depth of capture of *M. robusta* of 514 m. The species is found in slope waters from southern California northward around the Pacific rim to Japan. It has been reported from the stomachs of sperm whales from central California (Rice 1963b), western Canada (Clarke and MacLeod 1980), the Gulf of Alaska and Aleutian Islands (Okutani and Nemoto 1964), the western and central Aleutian Islands (Kodolov 1972), the Kuril Islands (Betesheva and Akimushkin 1955), and Japanese waters (Kawakami

1980). Antonelis et al. (1987) and Condit and Le Bouef (1984) reported this species from the stomachs of elephant seals from California waters.

Gonatidae

Members of this large family are found in the subarctic and transitional waters of the North Pacific, the Bering and Chukchi seas, the Arctic Ocean, the North Atlantic, and in Antarctic waters. In the subarctic Pacific the family is represented by 4 genera and 19 nominal species (Okutani et al. 1988). Three of the four genera are present in the waters off central California: the genus *Gonatus* is represented by at least five species, *Gonatopsis by* one, and *Berryteuthis* by one or possibly two species.

***Gonatus* spp.** Four occurrences represented by single beaks, and one by a whole specimen, are recognizable as *Gonatus*, but presently cannot be identified to species.

***Gonatus pyros* Young, 1972** Two occurrences are represented by one lower beak each, and one by three lower beaks; LRLs are 4.5 mm (four specimens) and 5.0 mm (one specimen). *Gonatus pyros* has been taken in demersal tows as deep as 440 m, and in midwater opening-closing tows at depths of 750–790 m and 500–1000 m (Jefferts 1983). This species is found in the waters of the California Current system and northwestward to about 175°E in the Alaska Current.

***Gonatus berryi* Naef, 1923** Each of our samples consists of 1–5 lower beaks. LRLs of five of the largest specimens were in the size range 5.0–5.8 mm. Jefferts (1983) reported *G. berryi* from opening-closing midwater trawls as deep as 760–830 m, and from demersal trawls at 375–450 m. This species ranges from the California and Alaskan current systems into the southern Bering Sea (Jefferts 1983). *Gonatus berryi* has been reported from the stomach contents of elephant seals from San Miguel Island, California (Antonelis et al. 1987).

***Gonatus* sp. (cf. *G. fabricii* [Lichtenstein, 1818])** *Gonatus fabricii* has not been reliably identified in the North Pacific or its adjacent seas. However, beaks similar to those of *G. fabricii* have been reported from stomachs of marine mammals taken from the California Current system, as detailed below. We have beaks representing only one or two squids per occurrence. In this species-group, the upper beak can also be used for identification. LRLs are in the size range 6.2–8.8 mm, with a mean of 7.9 mm. Young (1972) in his description of *G. californiensis* mentioned that it is very similar to *G. fabricii* specimens from the Atlantic and *G. antarcticus* from Antarctic waters. Clarke (1986a) mentions the difficulty in separating the beaks of *G. fabricii* and *G. antarcticus*. Our beaks are a reasonable match with those of *Gonatus* sp. illustrated by Mead et al. (1982:12, fig. 9) from the stomach of a *Mesoplodon carlhubbsi* taken off California, and with those listed as *G. fabricii* by Clarke and MacLeod (1980) from the stomachs of sperm whales taken off western Canada. Fiscus took two of our beaks (NMML

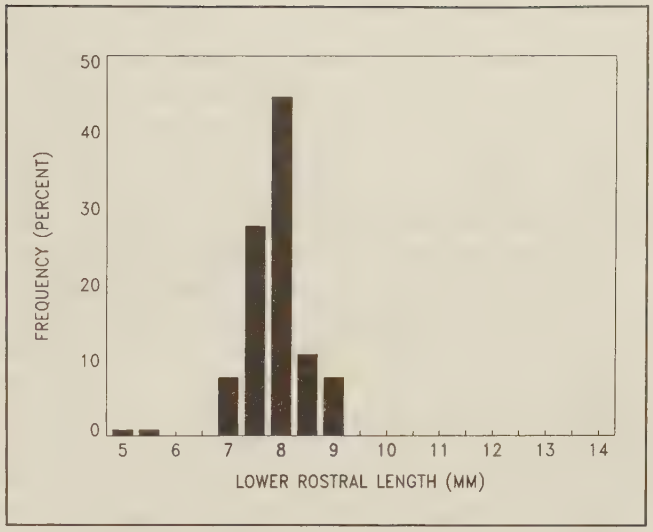

Figure 2
Lower rostral length-frequencies of 130 *Gonatopsis borealis* beaks from the stomachs of sperm whales taken off California.

136 and 137) to the Plymouth workshop in 1981. There they were examined by M.R. Clarke (Mar. Biol. Stn. U.K., Plymouth, England) who stated that they closely resemble the beaks of *G. fabricii* and *G. antarcticus* in the Marine Biological Association collections. The precise identification of these beaks must await the finding of comparably large beaks from known specimens of *G. californiensis*. For the present, most authorities are in agreement that *G. fabricii*, *G. antarcticus*, and *G. californiensis* are very similar morphologically, so we believe that they probably also have similar beaks.

***Gonatopsis borealis* Sasaki, 1923** This species ranked second in frequency of occurrence (66%) and first in total number of individuals. Most samples in which *G. borealis* occurred contained beaks of 1–8 squids, two samples each contained beaks of 10 squids, and three samples had beaks representing 11, 14, and 18 squids, respectively. Five complete specimens of *G. borealis* were obtained from the samples; four of these measured 202, 212, 230 and 320 mm ML. The crowns of 7 specimens were readily identified, as were the gladii of 19 specimens in the size range 255–318 mm GL. Gladius length closely approximates mantle length. Beaks removed from the whole specimens and crowns were used to identify the remaining beaks. The LRL of 130 beaks were in the size range 5.0–9.0 mm ($\bar{x}$ 7.9 mm) (Fig. 2). *Gonatopsis borealis* ranges across the subarctic waters of the North Pacific Ocean and Bering and Okhotsk seas, and in California Current waters as far south as Guadalupe Island, Mexico (Okutani et al. 1988, Young 1972, Fiscus unpubl. data). This species is mesopelagic to epipelagic, and some individuals migrate to the surface at night (Fiscus and Mercer 1982). This species has been taken in demersal tows between 85 and 650 m, and midwater opening-closing tows to 635–700 and 500–1000 m throughout the California and

Alaska currents (Jefferts 1983). The genus *Gonatopsis* has been reported in the stomachs of sperm whales around the Pacific rim. In the eastern Pacific only one species (*G. borealis*) is known. Rice (1963b) listed this species from central California. *Gonatopsis* is not listed from western Canada by Clarke and MacLeod (1980), but see below. Okutani and Nemoto (1964) listed *G. borealis makko* from the western Aleutians. Kodolov (1972) listed *G. borealis* from the western Aleutians and the Commander Islands. Betesheva and Akimushkin (1955) listed the genus *Gonatopsis* from the Kuril Islands. Okutani et al. (1976) listed two species, *G. octopedatus* and *G. makko*, from the Pacific Ocean off Honshu, Japan; and Okutani and Satake (1978) listed both *G. borealis* and *G. makko* taken from the same area off Japan one year later. In summary, the genus is an important component of the diet of sperm whales in the North Pacific, Bering, and Okhotsk Seas.

The beaks of *Gonatopsis borealis* and *Berryteuthis magister* are not separable except when very small (LRL <4.0 mm), when differences in the degree of wing darkening can be used in identifying some beaks. At the Plymouth workshop, Kubodera, Kristiansen, Fiscus, and others tried without success to find a means of differentiating between the two species; M.R. Clarke (Mar. Biol. Stn. U.K., Plymouth, England) likewise could not distinguish between the two. *Gonatopsis borealis* and *B. magister* occupy much the same range in subarctic waters; however, *G. borealis* ranges much farther south in the California Current system. Mature *B. magister* range south to Oregon waters; however, Jefferts (1983) identified two larval specimens from collections off central California. The smaller *B. anonychus* occupies much the same range as the two aforementioned species and occurs south to Monterey Bay, California (Anderson 1978). *Berryteuthis anonychus* beaks can be readily separated from the beaks of the other two species at most stages of growth. Kubodera and Jefferts (1984) listed the MLs of the largest known specimens of the three species: *G. borealis*, 480 mm; *B. magister*, 335 mm; and *B. anonychus*, 150 mm. We justify calling the central California beaks *G. borealis* because 31 positive identifications were made from 5 complete specimens, 7 crowns, and 19 gladii, all from near-adult or adult sized squids. At present, there are no specimens of adult or near-adult sized *B. magister* from central California waters; if mature *B. magister* are later identified from these waters, we may have to reconsider our identification of these beaks. The beaks listed as *B. magister* from the stomachs of sperm whales taken off western Canada (Clarke and MacLeod 1980) may include some *G. borealis*, based on the results of our examination of beaks of both species at the Plymouth workshop.

Unidentifiable Gonatids Four occurrences of single beaks or beak fragments were recognizable only as gonatids.

Architeuthidae

***Architeuthis japonica* Pfeffer, 1912** Beaks representing single squids were found in 11 stomach samples. These included seven upper beaks, three lower beaks, and one pair. Original identification was verified by M.C. Mercer and F.A. Aldrich (Fiscus and Rice 1974). (One occurrence—two pairs of beak fragments—originally listed as *Architeuthis* were later found to represent *Mesonychoteuthis hamiltoni*.) LRLs of the only three measurable lower beaks were 11.0, 12.0, and 12.5 mm. The known distribution of the giant squid in the North Pacific through 1973 was summarized by Fiscus and Rice (1974). The only record from California waters at that time was that of Pinkas et.al. (1971). Since 1973, a number of *Architeuthis* have stranded or been captured in trawls along the west coast of the United States from Santa Barbara, California, north to Oregon (F.G. Hochberg, Santa Barbara Nat. Mus. Hist., Santa Barbara CA 93105, pers. commun. 24 Aug. 1987). Hochberg stated that *Architeuthis* from around the Pacific rim from California to Japan can all be attributed to the species *A. japonica*, and we have listed our specimens as such. Clarke (1986a) stated that this genus is found in the Atlantic, Pacific, and Indian Oceans south to the subtropical convergence. Roper and Boss (1982) presented a review of what is known of the biology and habits of this genus. *A. japonica* has been identified from sperm whale stomachs at various locations around the Pacific rim: central California (Fiscus and Rice 1974), the western Aleutian and Commander islands (Kodolov 1972), the Kuril Islands (Betesheva and Akimushkin 1955), and Honshu, Japan (Okutani et al. 1976).

Histioteuthidae

Three species of histioteuthids have been described from the eastern North Pacific: *Histioteuthis corona berryi*, *H. dofleini*, and *H. heteropsis* (Voss 1969). Young (1972) and Jefferts (1983) listed records from California waters. The three published records of *H. c. berryi* are not from the whaling area off central California (Voss 1969, Jefferts 1983). Histioteuthids were identified from 73 of the 157 samples (46%) (in four samples more than one species was identified). Histioteuthids have been reported from the stomachs of sperm whales taken around the Pacific rim: off western Canada (Clarke and MacLeod 1980), the western Aleutian Islands (Okutani and Nemoto 1964), the western Aleutian and Commander islands (Kodolov 1972), and Honshu, Japan (Okutani et al. 1976, Okutani and Satake 1978).

***Histioteuthis* spp.** Beaks representing 1–7 squids per sample were identified. Twelve of the occurrences listed as *Histioteuthis* spp. are from 1970 samples which were misplaced and could not be reexamined in 1987–88. Beaks in this category are most likely *H. dofleini* or *H. heteropsis*.

***Histioteuthis dofleini* (Pfeffer, 1912)** One entire specimen (NMML 59) was identified by C.F.E. Roper (Natl. Mus. Nat. Hist., Smithson. Inst., Wash., D.C. 20560). In addition to this specimen, two crowns and a number of buccal masses were identified. The remaining 53 occurrences are represented by 1–12 beaks per sample. LRLs of 21 beaks were in the size range 3.0–7.0 mm. Jefferts (1983) reported taking this species in demersal tows to maximum depths of 100–200 m and 2700–3700 m, and in opening-closing midwater tows as deep as 500–600 m.

***Histioteuthis heteropsis* (Berry, 1913)** In five samples single beaks represented each occurrence, and in one sample beaks representing four squids were identified. Jefferts (1983) reported taking this species in both midwater and demersal tows at depths of 0–500 m. Identification and separation of the beaks of *H. heteropsis* from *H. dofleini* were based on descriptions and illustrations by Wolff (1984).

Ommastrephidae

Two large ommastrephids are present at least seasonally or periodically off the California coast: *Ommastrephes bartrami* and *Dosidicus gigas* (Young 1972, Anderson 1978, Wolff 1984). Beak differences between the two genera are slight.

***Dosidicus gigas* (d'Orbigny, 1835)** In comparing beaks from the sperm whale stomachs with those from whole specimens in the NMML collection, the four lower beaks from whale stomachs are a better match with *D. gigas* (NMML 92) than with *Ommastrephes bartrami*. Anderson (1978), citing other authors and his own observations, stated that *D. gigas* specimens from Monterey Bay, California, generally measured less than 350 mm ML. His northernmost capture record was about 20 miles north of Santa Cruz, California. Hochberg and Fields (1980) and Erhardt et al. (1983) presented additional life-history information on *D. gigas*. LRLs of the four beaks which we consider to be *D. gigas* were 2.7, 3.0, 3.0, and 5.5 mm. Wormuth (1976) reported that specimens taken north of the Equator were much smaller than those taken south of the Equator. Of more than 800 northern specimens measured, only five exceeded 300 mm ML; whereas off Peru, specimens of 1.50 m ML are not uncommon (Clarke et al. 1976). Clarke et al. (1976) report beaks 10–30 mm LRL in the stomachs of sperm whales taken in the Humboldt Current off Chile and Peru, where this species constitutes the bulk of the diet of sperm whales (Clarke et al. 1988). Two specimens in the NMML collection taken north of the Equator measured 167 and 378 mm ML, and 3.5 and 5.8 mm LRL, respectively.

Unidentifiable Ommastrephid One large upper beak can be listed only as an ommastrephid. Around the Pacific rim, *Ommastrephes bartrami* has been reported in sperm whale stomachs from western Canada (Clarke and MacLeod (1980) and from Honshu, Japan (Okutani et al. 1976, Okutani and Satake 1978), and an unidentified ommastrephid has been reported from the Kuril Islands (Tarasevich 1963).

Chiroteuthidae

***Chiroteuthis calyx* Young, 1972** Three species of this family have been collected off California—*Chiroteuthis calyx*, *Valbyteuthis oligobessa*, and *V. danae*—although the latter is a tropical species that is only a straggler to southern California waters (Young 1972, Anderson 1978). There are some indications that *Valbyteuthis* lives at greater depths than Chiroteuthis (Roper and Young 1975). No *Valbyteuthis* beaks were available in the NMML collection to compare with beaks from the sperm whale stomach samples. Beaks from our samples are quite similar to chiroteuthid beaks from elephant seal stomachs obtained at San Miguel Island, California (Fiscus, in prep.). Although they resemble the *Valbyteuthis* beaks illustrated by Clarke (1986a, fig. 86B), they are not a good match for the *Valbyteuthis* beaks figured by Roper and Young (1967, plate 4). They are in reasonable agreement with the *Chiroteuthis* beaks illustrated by Clarke (1986a, fig. 86(A)). The crest line and lateral wall in our specimens appear to be longer than those of *C. calyx* in the NMML collection, somewhat similar to *Chiroteuthis* sp. B of Clarke et al. (1976, fig. 5). Elsewhere around the Pacific rim, chiroteuthids have been reported in the stomachs of sperm whales taken off western Canada (Clarke and MacLeod 1980) and off Honshu, Japan (Okutani and Satake 1978), and *Chiroteuthis veranyi* has been reported from the western Aleutian and Commander islands (Kodolov 1972) and from the Kuril Islands (Betesheva and Akimushkin 1955).

Mastigoteuthidae

***Mastigoteuthis* spp.** Two species of this genus are known from the eastern North Pacific, *M. pyrodes* (Young 1972) and *M. dentata* (Jefferts 1983). Fiscus took an unidentified lower beak (NMML 149) to the Plymouth workshop in 1981, where it compared favorably with *Mastigoteuthis* specimens in the Marine Biological Association collections. The beak was later examined by M.R. Clarke (Mar. Biol. Stn. U.K., Plymouth, England) who stated it matched his ?*Mastigoteuthis* species B (see Clarke 1980). Three other lower beaks from two different samples were later judged by Fiscus to belong to this genus. LRLs for all four beaks are 5.5, 6.0, 6.5, and 8.0 mm. Mead et al. (1982) reported finding seven lower and eight upper beaks of *M. pyrodes* in the stomach of a *Mesoplodon carhubbsi* which had stranded near San Diego, California. The LRLs of these beaks measured 3.4–3.8 mm. Clarke and MacLeod (1980) reported the occurrence of one ?*Mastigoteuthis* sp. from the stomach of a sperm whale taken off western Canada. The genus has not been reported from sperm whale stomachs elsewhere around the Pacific rim.

Cranchiidae

At least eight species of cranchiids, representing seven genera, have been reported from the eastern North Pacific; most of these are present in the California Current system.

***Taonius pavo* (Lesueur, 1821)** This species is represented by two lower beaks with LRLs of 7.2 and 8.5 mm. It has been reported by Young (1972) and Jefferts (1983) in the California Current system. Voss (1980) describes the distribution of the genus as circumglobal in subantarctic to subarctic waters, mainly at depths greater than 200 m. In California waters, *Taonius pavo* has been reported from the stomachs of elephant seals at San Miguel Island, California (Antonelis et al. 1987). Around the Pacific rim, *Taonius* spp. have been reported from stomachs of sperm whales taken off western Canada (Clarke and MacLeod 1980), in the western Aleutian Island area (Okutani and Nemoto 1964), in the western Aleutian and Commander Islands (Kodolov 1972), in the Kuril Islands (Betesheva and Akimuskin 1955), and off the coast of Honshu, Japan (Okutani et al. 1976, Okutani and Satake 1978).

***Megalocranchia* spp.** *M. speculator* has been reported by Jefferts (1983) from the central Pacific north of the Hawaiian Islands. To our knowledge, there are no specimen records of *Megalocranchia* spp. from the California Current system. Voss (1980) reported a circumglobal distribution in tropical and subtropical waters, and a depth distribution from subsurface to deeper than 1000 m. One of our lower beaks (NMML 274) was taken to the Plymouth workshop. M.R. Clarke (Mar. Biol. Stn. U.K., Plymouth, England) stated that this beak is *Megalocranchia*; F.G. Hochberg (Santa Barbara Nat. Mus. Hist., Santa Barbara, CA 93105) also examined this specimen and is in agreement with Clarke. Fiscus' identification of other beak samples is based on comparisons with this beak and with illustrations published by Clarke (1986a). LRLs of six specimens were 6.5, 7.0, 14.0, 14.5, 15.0, and 15.5 mm. Clarke (1980), who at that time called this genus *Phasmatopsis*, reported its occurrence in the stomachs of sperm whales taken at Durban and Donkergat, South Africa; Albany, western Australia; South Georgia; and from Antarctic waters. It has not been previously reported from sperm whale stomachs around the Pacific rim.

***Galiteuthis* spp.** Two species of *Galiteuthis* occur in the California Current system, *G. phyllura* and *G. pacifica* (Young 1972, Jefferts 1983, Voss 1980). Voss (1980) reported that the genus has a circumglobal distribution from antarctic to subarctic waters, and that it occurs from subsurface waters to depths of 1500 m. We found *Galiteuthis* specimens in 57 (36.3%) of the stomachs. Most could not be identified to species. These included several crowns and buccal masses, one gladius measuring 445 mm GL, and beaks representing 1–5 squids per sample. LRL measurements of seven of these beaks were in the size range 5.0–7.0 mm. Around the Pacific rim, *Galiteuthis* spp. have been reported from the stomachs of sperm whales from British Columbia (Clarke and MacLeod 1980), off the western Aleutian Islands (Okutani and Nemoto 1964), off the western Aleutian and Commander Islands (Kodolov 1972), off the Kuril Islands (Betesheva and Akimushkin 1955), and off Honshu, Japan (Okutani and Satake 1978). They have also been reported from elephant seal stomachs at San Miguel Island, California (Antonelis et al. 1987).

***Galiteuthis phyllura* Berry, 1911** Fiscus took two lower beaks (NMML 215) to the Plymouth workshop. M.R. Clarke (Mar. Biol. Stn. U.K., Plymouth, England) examined these beaks and agreed that they were *Galiteuthis*, most probably *phyllura*. These two beaks had LRLs of 5.8 and 6.0 mm. The remaining eleven occurrences listed here are based on comparisons of these two beaks and other *Galiteuthis* specimens in the samples. Roper and Young (1975) mention that *G. phyllura* larvae move deeper as they develop in size, and at approximately 60 mm ML larval development is complete and they descend to 900 m or more. *Galitenthis pacifica* off Hawaii exhibit similar characteristics, and most occupy depths below 600 m both day and night (Roper and Young 1975). The species ranked second in abundance of the cephalopods taken in 63 midwater trawl samples taken in Monterey Bay, California (Anderson 1978).

***Galiteuthis pacifica* Robson, 1948** Fiscus took one pair of beaks from a crown (NMML 127b) to Plymouth. M.R. Clarke (Mar. Biol. Stn. U.K., Plymouth, England) examined the lower beak and said it most closely resembled *G. pacifica*. Beaks representing 1–3 squids per sample were identified by Fiscus based on this specimen. LRLs of two beaks were 5.0 and 5.5 mm.

***Mesonychoteuthis hamiltoni* Robson, 1925** Two pairs of beak fragments (NMML 121) had LRLs of 30.0 and 32.0 mm. They were taken from the stomach of a 16.2-m male sperm whale, killed on 19 October 1970 and one of the largest taken in the Richmond whaling operations. Rice and Wolman (1970) estimate its age at 36 years on the basis of annual growth layers counted in a mandibular tooth. These beaks were originally identified as *Architeuthis* sp. by Fiscus, and were included in the samples described by Fiscus and Rice (1974). These beaks have much larger LRLs than the three lower beaks of *Architeuthis* sp. (11.0, 12.0, and 12.5 mm). Fiscus took these beaks to the Plymouth workshop where they were examined by M.R. Clarke (Mar. Biol. Stn. U.K., Plymouth, England) who stated, "After much careful consideration I now feel quite certain that the lower jaws are not *Architeuthis* but are definitely *Mesonychoteuthis*, this in spite of the locality of collection. As far as we know this species does not live north of lat. 40°S and these beaks certainly look as if they have been in the whale's stomach for a very long time." These *Mesonychoteuthis* beaks strongly suggest the movement of at least one sperm whale from a southern- to a northern-hemisphere feeding ground. Ivashin (1967) reported that a male sperm whale (body length 10.4 m) tagged at lat. 21°33′N was recovered 4.25 years later at 33°20′S in the Atlantic Ocean. This is the only evidence to date of long-distance transequatorial migration by sperm whales.

Clarke (1986a) mentions that *M. hamiltoni*, the only species of its genus, has a circumpolar Antarctic distribution, and that it forms a large portion of the sperm whale diet in that region. He mentions beaks with LRL peaks at 12.0 and 25.0 mm, and off the South Shetlands at 36.0 mm; his largest specimen measured had an LRL of 48.0 mm. The largest specimen caught in an opening-closing net was taken at 2000 m measuring 1050 mm ML and 22.0 mm LRL. Additional information on this species was given by Clarke (1980).

Unidentifiable Cranchiids We list nine occurrences only as cranchiids; two of these are represented by gladii only, one by a lower beak distinguishable only as a cranchiid. The remaining six occurrences are from the 1970 samples which were not reexamined in 1987–88; they were most likely *Galiteuthis* spp.

Vampyroteuthidae

***Vampyroteuthis infernalis* Chun, 1903** Beaks representing 1–4 specimens were found in 43 whale stomachs. Both upper and lower beaks can be identified. Hood length measurements from 10 lower beaks were 9.0. 11.0, 11.0, 11.5, 12.0, 12.5, 13.0, 13.5, 14.0, and 14.0 mm. *Vampyroteuthis infernalis* is the only species in the family. The vampire-squid is described as an inhabitant of the abyssopelagic zone by Voss (1967). Young (1972) and Jefferts (1983) report this species from California Current waters. Roper and Young (1975) report the upper limit of most captures at 600 m and a lower limit of 1100–1200 m. The species has been reported from the stomachs of sperm whales taken off western Canada (Clarke and MacLeod 1980), but not from other locations around the Pacific rim. It has been found in the stomachs of elephant seals at San Miguel Island, California (Antonelis et al. 1987). Clarke (1980) reported specimens from the stomachs of sperm whales taken at Durban and Donkergat, South Africa, with hood lengths similar to our specimens.

Octopodidae

***Octopus dofleini* (Wulker, 1910)** Eleven of our samples each contained 1–5 beaks. Measurements of three lower beaks were:

Hood length	Crest length
18.0 mm	41.5 mm
16.2	37.8
16.0	37.8

The life history and range of the giant octopus have been described by Hartwick (1983). Hochberg and Fields (1980) report the eastern North Pacific subspecies *O. d. martini* ranges from British Columbia south to Monterey, California, at depths to 100 m, and an unnamed subspecies from off the California Channel Islands and San Diego. Anderson (1978) and Talmadge (1967) report this species from Monterey Bay and northern California. Clarke and MacLeod (1980) report two octopods from the stomach of a sperm whale taken off western Canada, with hood lengths of 12.5 and 13.3 mm, which no doubt represent *O. dofleini*. Betesheva and Akimushkin (1955) report this species (under the name *O. gibertianus*) from sperm whales taken off the Kuril Islands.

Alloposidae

***Alloposus mollis* Verrill, 1880** One occurrence of two beaks and one represented by one beak. Measurements of two lower beaks were:

Hood length	Crest length
13.0 mm	24.0 mm
13.0	27.0

The family Alloposidae is represented by this single species. Young (1972) took one specimen from the Santa Catalina basin of southern California. F.G. Hochberg (Santa Barbara Mus. Nat. Hist., Santa Barbara, CA 93105, pers. commun. 21 Oct. 1988) mentioned several unpublished California records from the Santa Barbara Natural History Museum and Berry collections. Roper and Young (1975) report this species from Hawaiian waters. Thore (1949) said that this species is restricted to tropical and subtropical waters throughout the world. Akimushkin (1965) reports it in the Pacific between lat. 40°N and 40°S, and lists it as bathypelagic abyssal in habit. Roper and Young (1975) report this species has been taken from the surface to depths of 3180 m. *Alloposus mollis* has been reported from the stomachs of sperm whales taken off the Kuril Islands (Betesheva and Akimuskin 1955), off Durban and Donkergat, South Africa (Clarke 1980), and from the Tasman Sea (Clarke and MacLeod 1982).

Unidentifiable Beaks

We have separated this category into three groups:

Group 1 Nineteen occurrences represented mostly by unidentifiable fragments and upper beaks.

Group 2 Sixty-seven occurrences represented by upper beaks which can be attributed to two families, Histioteuthidae and Cranchiidae.

Group 3 Four occurrences represented by upper beaks which can be attributed to either of two genera—*Megalocranchia* (family Cranchiidae) or *Taningia* (family Octopoteuthidae).

Table 2

Families of cephalopods identified from stomachs of deep-diving marine mammals from the west coast of the United States (except Alaska) and Canada.

	Physeter macrocephalus		*Mirounga angustirostris*		*Mesoplodon carlhubbsi*
Cephalopod family	Central California[1]	British Columbia[2]	Southern California[3]	Central California[4]	Southern California[5]
Loliginidae	X				
Enoploteuthidae	X		X		
Octopoteuthidae	X	X	X	X	X
Onychoteuthidae	X	X	X	X	X
Cycloteuthidae		X			
Gonatidae	X	X	X	X	X
Architeuthidae	X				
Histioteuthidae	X	X	X	X	X
Ommastrephidae	X	X			
Chiroteuthidae	X	X	X	X	
Mastigoteuthidae	X				X
Cranchiidae	X	X	X	X	
Vampyroteuthidae	X	X	X		
Octopodidae	X	X	X	X	
Ocythoidae		X			
Alloposidae	X				

[1]Present study
[2]Clarke and MacLeod 1980
[3]Antonelis et al. 1987
[4]Condit and Le Boeuf 1984
[5]Mead et al. 1982

Discussion

Berzin (1972), Kawakami (1980), and Clarke (1980) have provided lists of cephalopods identified from the stomachs of sperm whales from various locations around the world, and Rice (1989) has cited the major regional studies of sperm whale food habits. Clarke (1980) corrected or updated older records to conform to current nomenclature, making his account particularly useful.

Around the world, the same cephalopod families contribute to the sperm whale's diet, varying somewhat for each locality. With few exceptions, the larger, deeper-living species contribute most to the diet. Since the above authors have documented these, we do not add a similar compilation. We have felt it useful to document published records of cephalopods identified from the stomachs of deep-diving marine mammals along the west coast of the United States (excluding Alaska) and Canada (Table 2).

Recent feeding by sperm whales captured off central California is demonstrated by the presence of cephalopod flesh in their stomachs. Families represented by the presence of entire squids include Onychoteuthidae (*Moroteuthis*), Gonatidae (*Gonatopsis*), and Histioteuthidae (*Histioteuthis*); in addition, Cranchiidae (*Galiteuthis*) is represented by buccal masses. Ranked by frequency of occurrence, *Moroteuthis* (113) was identified in 72% of the 157 samples, *Gonatopsis* (104) in 66%, *Histioteuthis* (73) in 47%, and *Galiteuthis* (62) in 36%.

All the genera reported in this paper, with three exceptions (*Taningia*, *Megalocranchia*, and *Mesonychoteuthis*), have been taken by various types of sampling nets or commercial trawl nets in the California Current system. Marine mammals still remain the best sampling device for capturing adult and near-adult sized specimens.

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